

Reproductive Potential of Bisexual *Pycnoscelus indicus* and Clones of Its Parthenogenetic Relative, *Pycnoscelus surinamensis*¹

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ABSTRACT

Five reproductive characters of bisexual *Pycnoscelus indicus* (F.) and 12 parthenogenetic clones of *Pycnoscelus surinamensis* (L.) (5 chromosomal forms) were compared. In both species maturation of basal oöcytes and development and hatching of the eggs in the oötheca is less than 100 percent. *P. indicus* is a better reproducer

than any of the *P. surinamensis* clones. Reproductive potential varies between different clones of *P. surinamensis* but this is not necessarily correlated with changes in chromosome number, i.e., clones with similar numbers of chromosomes may differ in their reproductive potential.

The parthenogenetic and bisexual forms of the Surinam cockroach, *Pycnoscelus surinamensis* (L.) (Roth and Willis 1961), are considered to be sibling species, the specific name *surinamensis* being retained for the parthenogenetic species, and the name *P. indicus* (F.) being applied to the bisexual form (Roth 1967). Both species are polymorphic with regard to chromosome numbers (Roth and Cohen 1968). *P. indicus* from Hawaii has $2n$ (δ) = 35 or 37, and $2n$ (♀) = 36 or 38. I have a third chromosomal form with 34 (♀) chromosomes from Sakaerat, Thailand (collected by S. Supachai and Sukhum, Sept. 13, 1967), but have been unable to establish a large colony. This culture was started by crossing a Thai-land female with a Hawaiian male. At least 8 different chromosome numbers are known for about a dozen clones of *P. surinamensis* from different geographical localities (Table 1). Not shown in the table is a clone with 35 chromosomes from Thailand (started from nymphs and adults I collected under a house in Pak Thong Chai, 6 April 1967), but there were too few individuals in the culture to include in this study. In addition to these *surinamensis* clones, Matthey (1945, 1948) reported a form which originated from Kuala Lumpur, Malaysia, with 38 (♀) chromosomes, and Suomalainen (1945) claimed that specimens from the same source (botanical garden and crocodile house in Berlin) had 36 (♀) chromosomes. I do not have clones with these chromosome numbers.

"In all parthenogenetic animals the diploid bisexual race is the original, from which the parthenogenetic races have developed" (Suomalainen 1962). Some *surinamensis* clones probably arose polyphyletically by polyploidy and/or aneuploidy (Roth and Cohen 1968). I consider *surinamensis* clones with 34, 36, or 38 chromosomes to be diploid forms probably arising from *P. indicus* with $2n$ (♀) = 34, 36, or 38 chromosomes; females with 35, 37, or 39 chromosomes are diploid-aneuploid (these could have arisen from bisexual females with 34, 36, or 38 chromosomes or from other aneuploid forms). Clones with 54 chromosomes are considered to be triploids, possibly arising from *indicus* which had $2n$ (♀) = 36 chromosomes; clones with 53 chromosomes are considered

to be triploid-aneuploid, probably resulting from the triploid clone.

Although parthenogenesis is considered to be a dead end from an evolutionary viewpoint, *P. surinamensis* is a common species in the tropics and is apparently highly successful. Certain clones differ morphologically in size (Fig. 1) and color and are easily recognizable (e.g., Bogor nymphs are red compared to the usual black color of nymphs of other clones; adult females from Luang Cave, Thailand, have black tegmina, whereas other clones with intensive coloration are blackish, chestnut brown, the marginal field ochraceous-buff, wholly, or in part, suffused with blackish chestnut brown).

I believe that *P. indicus* was the parent stock from which *P. surinamensis* arose (Roth 1967). It is unknown how frequently individuals of *P. indicus* become parthenogenetic, but I have never seen *surinamensis* develop in *indicus* cultures in the 20 years I have maintained Hawaiian *indicus*. Over the years I have noted that certain clones of *P. surinamensis* did not increase in numbers as readily as others, suggesting that not all of the forms reproduce equally well. Roth and Willis (1961) compared certain biological characters of *P. indicus* from Hawaii with those of *P. surinamensis* from Florida and found that slightly fewer eggs hatched from *surinamensis* oöthecae.

The purpose of this paper was to compare the biotic potential of bisexual *P. indicus* with that of parthenogenetic *P. surinamensis* and to determine whether or not various chromosomal forms of *surinamensis* differ in reproductive capacity. The following characters were studied: 1) number of ovarioles; 2) number of basal oöcytes in each ovariole which mature; 3) number of eggs deposited in an oötheca; 4) number of oöthecal eggs which develop; and 5) number of eggs which hatch. The factors of nymphal development and survival, which would also contribute to biotic potential, were not investigated.

MATERIAL AND METHODS

The insects were reared on Purina Lab Chow at about 26°C and about 70% R.H. All measurements were made on females isolated at emergence and kept for various periods of time. The number of ovarioles was determined on females shortly before oviposition

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(about one week after emergence) so that those oöcytes which did not mature could be counted. Counts of the number of eggs laid were obtained from oöthecae removed from the uterus shortly after oviposition. The number of uterine eggs which developed was determined from oöthecae removed from the female shortly before parturition (usually about 40 days after oviposition). Developed uterine eggs were those with well developed embryos; undeveloped eggs did not increase in size and contained no visible embryos. All observations were based only on the first oötheca formed.

Two colonies of *P. indicus* were used. One was started in 1954, with additional material obtained in 1958, originating from Barber's Point and Koko Head, Oahu, Hawaii, sent by Mr. Fred A. Bianchi. The second was started from 6 females from Bogor, Indonesia, received from Dr. S. Kadarsan in March 1965; these were mated to Hawaiian males since no Indonesian males were available. The sources of starting material of the various clones of *P. surinamensis* are shown in Table 1.

RESULTS

Number of Ovarioles and Basal Oöcytes Which Mature.—The mean number of ovarioles in *P. indicus* was 43 (Table 2). The diploid clones (34 chromosomes) of *P. surinamensis* had the same, or higher, average number of ovarioles than *indicus*. Four of the 6 triploid (54 chromosomes) or triploid-aneuploid

forms (53 chromosomes) had an average number of ovarioles in the 40's but 2 clones (USF[a] and JMP) had a reduced number, averaging 33 ovarioles. The number of basal oöcytes which matured in the diploid approximate that of *P. indicus* and is higher than the number which matured in diploid-aneuploid, triploid, or triploid-aneuploid forms (Table 2). Ninety-four percent of the basal oöcytes of the ovarioles matured in *P. indicus*. In the diploid, and in one diploid-aneuploid (IB) form of *P. surinamensis*, 82 to 94% matured. With the exception of the USF(b) clone (81%), there was a sharp drop in the number of oöcytes which matured in the triploid, triploid-aneuploid, and one diploid-aneuploid (BP) forms, the percentage ranging from 64 to 71 (Fig. 2). The clones with similar numbers of ovarioles and similar numbers of basal oöcytes which matured are grouped in Table 4.

In many clones, most of the oöcytes which failed to develop remained very small and had little or no yolk in them. However, in the Jamaica clone (JMP), of 17 females which failed to oviposit within 2 weeks, 7 had small oöcytes with yolk and 10 had large oöcytes (but not mature), some or all of which were being resorbed. Twelve JMP females aborted their oöthecae without first retracting them into the uterus.

Number of Eggs in the Oötheca and Number Which Develop.—Only mature oöcytes are oviposited so that the number of eggs in the oötheca depends upon the number of basal oöcytes which mature

Table 1.—Chromosome numbers and sources of *P. surinamensis* clones.

Clone Abbreviations	Chromosome number ^a	Source of starting material
AuFI	34	Australia, Fraser Island. Originally started February 1949 from one female at the Queensland Institute for Medical Research; some were eventually sent to CSIRO and I received specimens from the late Dr. I. M. Mackerras, 2 Nov. 1964.
BM	34	Brazil, Moura, Rio Negro, Amazonas. Several individuals collected by me 22 July 1967.
BST	34	Brazil, Serra Tamendauí, Rio Negro, Amazonas. Several individuals collected by me 16 July 1967, around a native hut.
TLCP	34	Thailand, Tam Khao Luang Cave, Petchburi. Several nymphs collected by me, April 1967.
IB	37	Indonesia, Bogor. Two nymphs received from Dr. S. Kadarsan, March 1965.
BP	39	Brazil, Puraquequara, Rio Negro, Amazonas. Two adult females collected by me at the Mission School, 31 July 1967.
BB	53	Brazil, Belém. Several nymphs collected by me at the Inst. Agronomique do Norte, 29 June 1967.
USF(a)	53	United States, Florida. May be a mixture of Clearwater specimens (started from 2 females collected by me in 1950) and additional material from Gainesville received from Dr. L. A. Hetrick in 1958.
USF(b)	53	United States, Florida. May be a mixture of the above specimens and some that were collected in Tampa by Marc Roth in 1968.
AfU	54	Africa, Uganda, Kampala. Several nymphs collected by Dr. Barbara Stay, December 1967, in Queen Elizabeth Park, Lake Edward.
JMP	54	Jamaica, Mount Plenty, 3 miles from Goshan, in cave in bat guano. One female received from Marc Roth, 22 March 1966.
PC	54	Panama, Changuinola. A single female received from Clyde Stephen, 4 Nov. 1964.

^a From Roth and Cohen 1968.

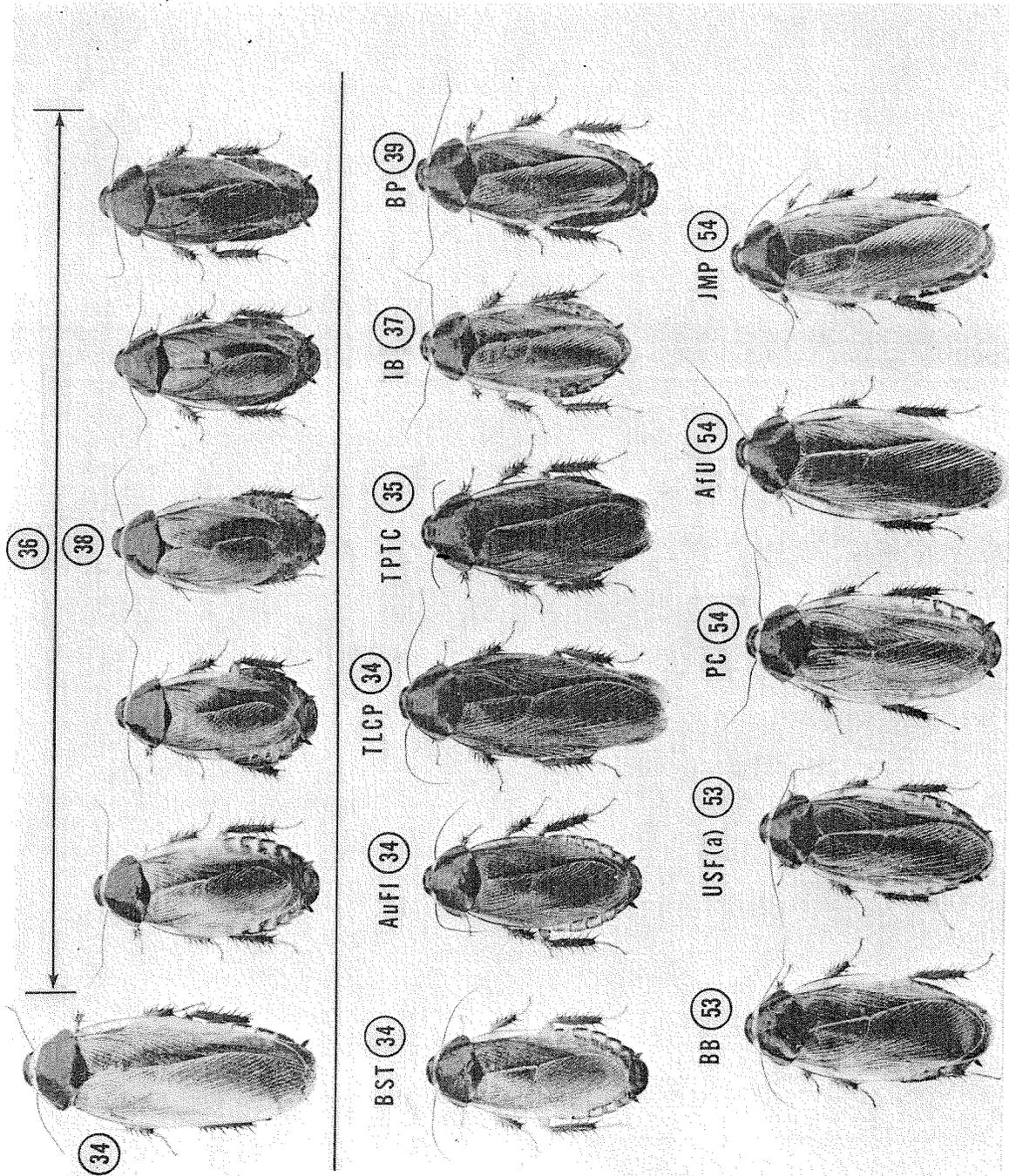


FIG. 1.—Examples of *P. indicus* (top row) and different clones of *P. surinamensis* (middle and bottom rows; see Table 1 for explanation of clone abbreviations). Female chromosome numbers shown in circles. *P. indicus* with 34 chromosomes (top row, left) is from Thailand. The other *P. indicus* with 36 or 38 chromosomes are from a culture started by crossing Indonesia (Bogor) ♀♀ × Hawaiian ♂♂.

Table 2.—Number of ovarioles and number of basal oöcytes which mature in *P. indicus* and clones of *P. surinamensis*.

Species and clones ^a	♀ Chromosome number ^b	Number of ovarioles (Mean ± SE)	Number of basal oöcytes which mature (Mean ± SE)	N
<i>P. indicus</i> ^c	36, 38	43.3±0.9	40.4±0.8	20
<i>P. surinamensis</i>				
AuFI	34	48.6±0.4	40.3±0.6	20
BM	34	47.4±1.5	43.8±0.6	20
BST	34	45.9±0.7	37.6±0.6	20
TLCP	34	41.3±1.1	38.7±1.2	15
IB	37	39.1±0.9	34.3±1.0	20
BP	39	42.1±0.7	27.2±1.1	20
BB	53	40.0±0.9	27.4±1.1	20
USF(a)	53	44.2±0.7	28.6±0.8	20
USF(b)	53	32.6±1.4	26.2±1.1	20
AfU	54	41.3±0.8	29.3±1.1	20
JMP	54	32.7±2.0	21.9±1.2	12
PC	54	43.6±0.8	31.0±0.8	20

^a See Table 1 for explanation of clone abbreviations.

^b From Roth and Cohen (1968).

^c Colony started by crossing bisexual Bogor ♀♀ × Hawaiian ♂♂. The numbers of ovarioles and maturing oöcytes for *P. indicus* are based on mated females. Similar determinations were made on 20 virgin females and the results did not differ significantly from those obtained from mated females (no. of ovarioles = 43.1 ± 0.8; number of oöcytes which matured = 38.8 ± 1.0).

The frequency distribution of numbers of eggs in the oöthecae is shown in Fig. 3 and 4. The average in *P. indicus* was 42 (Fig. 3). One diploid-aneuploid (IB) and the 4 diploid clones of *P. surinamensis* had numbers close to this value (Fig. 3, Table 3). One diploid-aneuploid (BP), and the 6 triploid, triploid-aneuploid clones have distinctly fewer eggs in their oöthecae (Fig. 3, Table 3). The number of oöthecal eggs which developed to an advanced embryonic stage was highest in *P. indicus* and significantly lower in all *surinamensis* clones (Tables 3, 4). Calculated on a percentage basis, however, several clones had high percentages of eggs which developed, equaling or approximating the 92% found in *P. indicus* (Fig. 5). The most striking examples of low egg development were those of the BM, AfU and JMP clones, where only 47, 60, and 52% of the eggs developed, respectively (Fig. 5). The clones with similar numbers of eggs in their oöthecae and number of eggs which developed are grouped in Table 4.

Hatch per Oötheca.—The number of eggs which hatched from an oötheca was the most variable character studied (Fig. 3 and 4). The average number of eggs which hatched was always less than the average number which developed into well-formed embryos (cf. Tables 3 and 5). The number of oöthecae with zero hatch varied considerably between clones and even between clones having similar chromosome numbers (Fig. 4).

One clone from Thailand (TLCP) was unusual in that 9 females (11%) everted their uteri at parturition (Fig. 6). The everted uterus was filled with internal tissue and could not be retracted again, mak-

ing further reproduction impossible. Uterine eversion was not observed in any other clones of *P. surinamensis* or in *P. indicus*.

DISCUSSION

The change from reproduction by fertilization to parthenogenesis requires that: a) the female be able to mature and lay eggs without mating, and b) the unfertilized eggs be able to develop (Suomalainen 1962). In cockroaches, maturation of the basal oöcytes is controlled by the corpus allatum hormone. Various members of the Blaberidae show decided differences in the external stimuli which control or influence the activity of these endocrine glands. In some, the brain apparently inhibits the corpora allata in virgin females and in these species the oöcytes do not develop at all or develop only partially, unless mating occurs. Examples are found in the Blaberidae which show all gradations from complete dependence on mating to species which do not require mating for the oöcytes to mature and be oviposited (Roth 1970).

In *P. indicus*, the oöcytes of virgins develop only slightly more slowly than mated females. The absence of mating does not affect the percentage of oöcytes which mature. The oöcytes of *P. surinamensis* develop at about the same rate in virgins or in females mated to males of *P. indicus* (Roth and Willis 1961).

The oöthecae of virgin *P. indicus* are almost always dropped (Table 6) without being retracted into the uterus (Roth and Willis 1961) and, therefore, this species cannot reproduce. *P. indicus* depends on the presence of sperm in the spermathecae for normal retraction of the oötheca (Stay and Gelperin 1966).

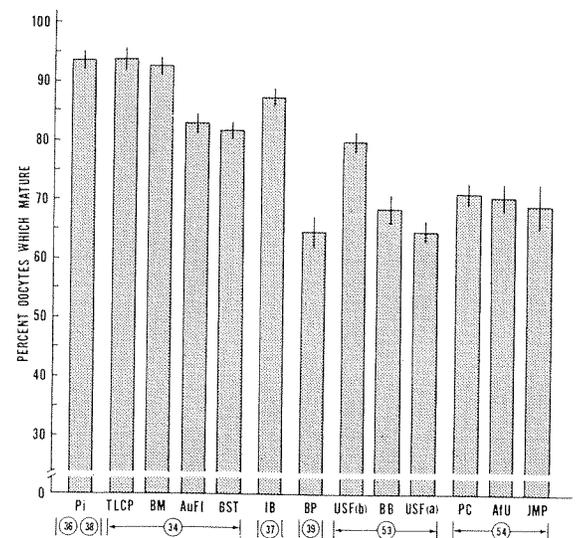


FIG. 2.—Variation in the percentage of basal oöcytes which mature in *P. indicus* and clones of *P. surinamensis*. (Pi = *P. indicus*; other abbreviations are clones of *P. surinamensis*, see Table 1. Chromosome numbers shown in circles. Vertical lines = standard errors).

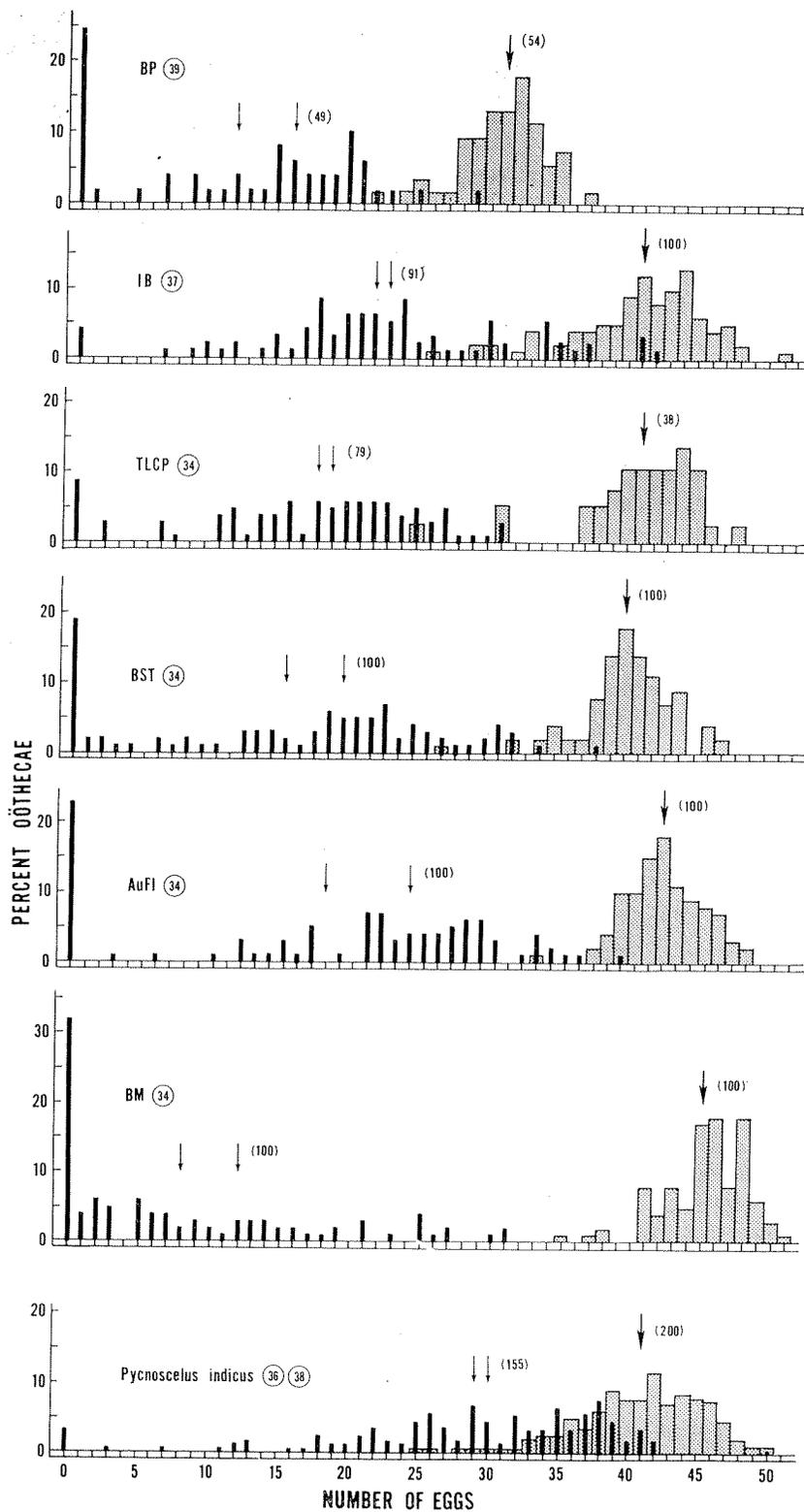


FIG. 3.—Frequency distribution of number of eggs in the oöthecae (stippled bars) and number which hatched (solid bars) in *P. indicus* and diploid, diploid-aneuploid clones of *P. surinamensis* (all graphs above *P. indicus*). Large arrows = mean number of eggs per oötheca. Small arrows = mean number of eggs which hatched per oötheca; of the two mean values shown, the lower value is based on all oöthecae examined (including zero hatch) and the higher is based only on oöthecae from which one or more eggs hatched. The numbers of oöthecae used are shown in parentheses to the right of the small and large arrows. See Table 1 for explanation of clone abbreviations. Number of female chromosomes shown in circles.

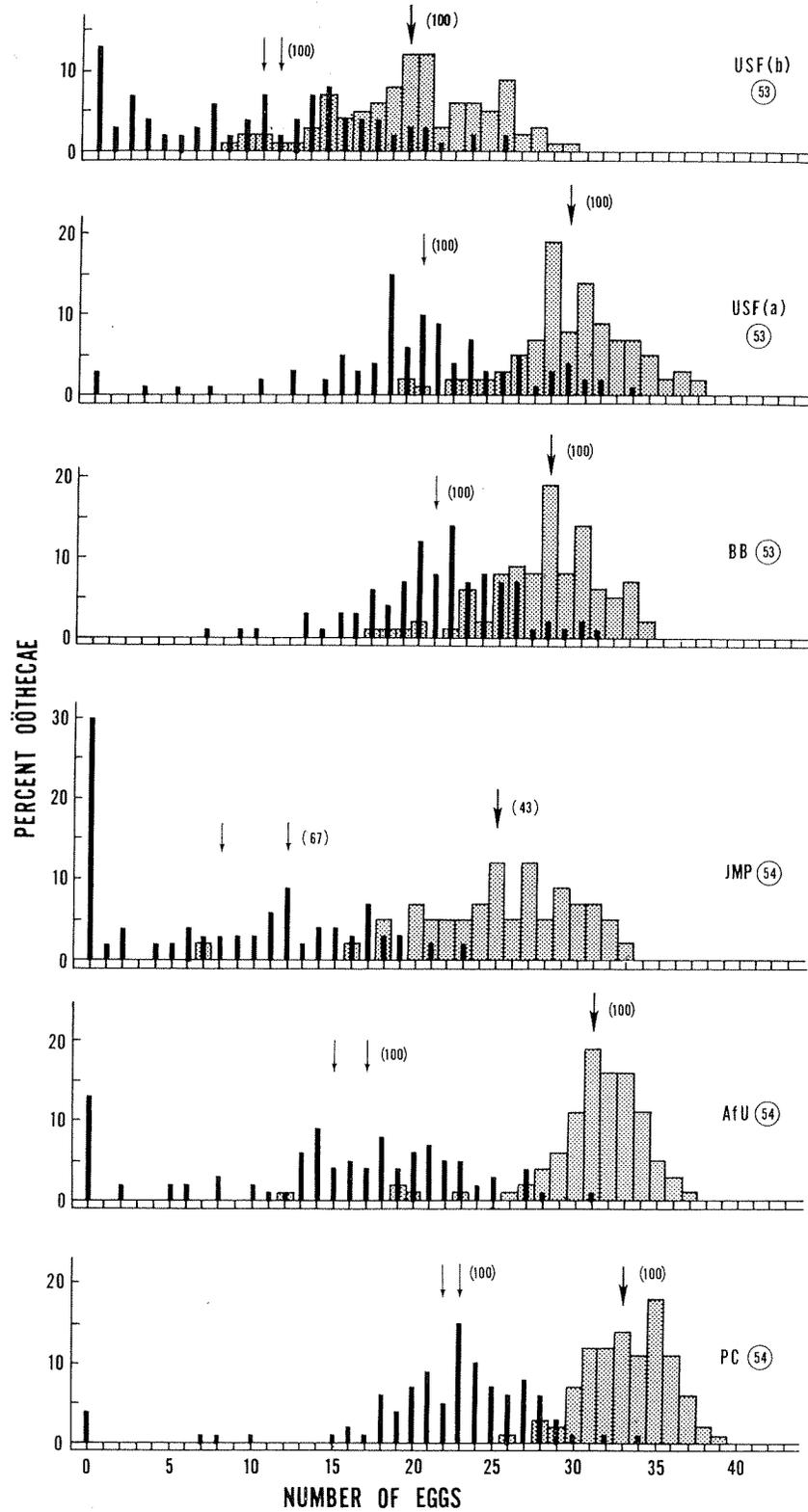


FIG. 4.—Frequency distribution of number of eggs in the oöthecae (stippled bars) and number hatched (solid bars) in triploid, triploid-aneuploid clones of *P. swinamensis*. (See Fig. 2 for explanation).

Table 3.—Number of eggs in the oötheca and number which develop in *P. indicus* and clones of *P. surinamensis*.

Species and clones ^a	♀ Chromosome number ^b	Number of eggs in oötheca (Mean ± SE)	Number of eggs which developed (Mean ± SE)	N
<i>P. indicus</i> ^c	36, 38	41.8±0.8	38.5±1.0	50
<i>P. surinamensis</i>				
AuFI	34	41.2±0.6	32.7±1.6	20
BM	34	44.9±0.8	21.6±2.0	20
BST	34	38.7±0.9	32.0±1.3	20
TLCP	34	41.8±0.6	29.7±1.4	15
IB	37	39.8±1.1	33.3±1.4	20
BP	39	31.0±0.6	27.2±0.9	20
BB	53	29.2±0.7	27.2±0.8	20
USF(a)	53	30.0±0.5	26.8±0.7	20
USF(b)	53	22.0±1.0	17.2±1.1	20
AfU	54	29.2±1.1	18.5±2.2	20
JMP	54	24.0±2.1	15.0±2.4	12
PC	54	33.2±0.5	29.2±1.0	20

^a See Table 1 for explanation of clone abbreviations.

^b From Roth and Cohen (1968).

^c Colony started by crossing bisexual Bogor ♀♀ × Hawaiian ♂♂.

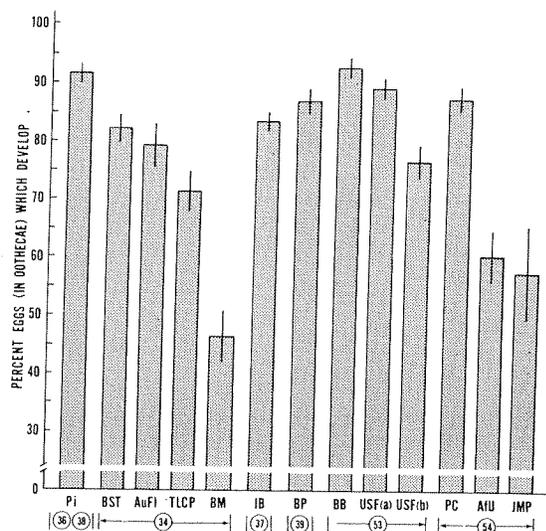


FIG. 5.—Variation in the percentage of oöthecal eggs which develop to late embryonic stage in *P. indicus* and clones of *P. surinamensis* (see Fig. 2 for explanation of symbols on the abscissa).

Table 4.—Grouping of *P. indicus* and clones of *P. surinamensis* in which reproductive characteristics were not significantly different ($P \leq .05$).

Groups	Character and similar clones	Mean number ^a (Range)
<i>Ovarioles in ovaries</i>		
I	JMP, USF(b)	32.6–32.7
II	IB, BB, AfU, TLCP	39.1–41.3
III	AfU, TLCP, BP	41.3–42.1
IV	BP, <i>P. indicus</i> , PC, USF(a)	42.1–44.2
V	USF(a), BST	44.2–45.9
VI	BST, BM	45.9–47.4
VII	BM, AuFI	47.4–48.6
<i>Basal oöcytes which mature</i>		
I	JMP	21.9
II	USF(b), BP, BB, USF(a), AfU	26.2–29.3
III	BP, BB, USF(a), AfU	27.2–29.3
IV	USF(a), AfU, PC	28.6–31.0
V	IB	34.3
VI	BST, TLCP	37.6–38.7
VII	TLCP, AuFI, <i>P. indicus</i>	38.7–40.4
VIII	BM	43.8
<i>Eggs in oötheca</i>		
I	USF(b), JMP	22.0–24.0
II	BB, AfU, USF(a), BP	29.2–31.0
III	PC	33.2
IV	BST, IB	38.7–39.8
V	IB, AuFI, TLCP, <i>P. indicus</i>	39.8–41.8
VI	BM	44.9
<i>Eggs in oötheca which develop</i>		
I	JMP, USF(b), AfU	15.0–18.5
II	USF(b), AfU, BM	17.2–21.6
III	USF(a), BP, BB, PC, TLCP	26.8–29.7
IV	TLCP, BST, AuFI, IB	29.7–33.3
V	<i>P. indicus</i>	38.5

^a Taken from Tables 2 and 3.

A necessary pre-condition for the evolution of parthenogenesis in *Pycnoscelus* was the acquisition of the ability to retract the oötheca in the absence of sperm. All of the clones of *P. surinamensis* used in this study have this capability; only in the Jamaica clone (JMP) is there a high of 25% abortion (Table 6). If the oöthecae of blaberids are not retracted quickly into the uterus, the enclosed eggs will desiccate and die (Roth and Willis 1955).

Table 5.—Hatching of eggs of *P. indicus* and various clones of *P. surinamensis*.

Species and clones ^a	♀ Chromosome number ^b	Number hatched ^c (Mean ± SE)	N
<i>P. indicus</i>	36, 38	28.8±0.8	155
<i>P. surinamensis</i>			
PC	54	22.0±0.6	100
IB	37	21.4±0.9	91
BB	53	21.1±0.4	100
USF(a)	53	19.7±0.6	100
AuFI	34	18.3±1.2	100
TLCP	34	16.6±0.9	79
BST	34	15.4±1.0	100
AfU	54	15.1±0.8	100
BP	39	11.3±1.2	49
USF(b)	53	9.8±0.7	100
JMP	54	8.2±0.9	67
BM	34	8.0±0.9	100

^a See Table 1 for explanation of clone abbreviations.

^b From Roth and Cohen (1968).

^c Brackets enclose clones which are not significantly different ($P \leq 0.05$).



FIG. 6.—A female (TLCP clone) with everted uterus (arrow) following parturition (ventral view). Line = 5 mm.

The dependence upon stimuli from sperm-filled spermathecae to retract the oötheca had to be lost before parthenogenesis could evolve in any species of Blaberidae. Although this has occurred in *P. suri-*

namensis, it is also occurring, in various degrees, in other blaberids. Species are known (Table 6) in which oöthecae from virgin females are either dropped (aborted), partly retracted, or are completely retracted into the uterus. Frequently the oöthecae of virgin female Blaberidae which are retracted into the uterus remain there for a variable period of time, though less than the gestation period, and are then aborted. The eggs in these oöthecae cannot develop completely, even if they had the ability to do so, because they would desiccate once outside the uterus. However, some females do retain their unfertilized eggs for the normal gestation period (and sometimes longer) and these would be the individuals which could evolve parthenogenesis. Thus, a few parthenotes have been found in *Byrotria fumigata* (Guérin) (Barth in Roth and Stay 1962) and *Nauphoeta cinerea* (Olivier) (Roth and Willis 1956; Springhetti and Cioci 1962).

A second prerequisite for parthenogenesis is the capacity of unfertilized eggs to develop and hatch. This ability is absent in *P. indicus* (in the small number of females which manage to retract their oöthecae) (Roth and Willis 1961). Though the unfertilized eggs of parthenogenetic *surinamensis* can develop, the ability to do so is not equally developed among all clones.

In *P. indicus* and all of the clones of *P. surinamensis* here studied, fewer basal oöcytes mature than there are ovarioles, fewer eggs develop than the number found in the oöthecae, and fewer eggs hatch than develop in an oötheca. Based on these characters, *P. indicus* has a higher biotic potential than any of the parthenogenetic clones of *P. surinamensis* (even

Table 6.—Oviposition behavior of virgin female Blaberidae.

Species	N	Oviposition behavior: oötheca		
		Aborted	Partially retracted	Completely retracted
<i>Pycnoscelus indicus</i> ^a	138	136 (99%)	0	2 (1%)
<i>Pycnoscelus surinamensis</i>				
Clones				
AuFI	100	1 (1%)	0	99 (99%)
BM	100	1 (1%)	0	99 (99%)
BST	100	1 (1%)	0	99 (99%)
TLCP	38	0	0	38 (100%)
IB	100	0	0	100 (100%)
BP	54	0	0	54 (100%)
BB	100	0	1 (1%)	99 (99%)
USF(a)	100	1 (1%)	0	99 (99%)
USF(b)	100	0	0	100 (100%)
AfU	100	3 (3%)	4 (4%)	93 (93%)
PC	100	0	2 (2%)	98 (98%)
JMP	55	14 (25%)	0	41 (75%)
<i>Byrotria fumigata</i> (Guérin) ^b	102	5 (5%)	5 (5%)	92 (92%)
<i>Nauphoeta cinerea</i> (Olivier) ^b	17	3 (18%)	4 (24%)	10 (59%)
<i>Blaberus cranii</i> Burmeister ^b	40	4 (10%)	23 (58%)	13 (32%)
<i>Leucophaea maderae</i> (F.) ^b	47	36 (77%)	0	11 (13%)

^a From Roth and Willis (1961).
^b From Roth and Stay (1962).

though several clones have a larger number of ovarioles), principally because in *P. indicus* the percentage of eggs which develop and hatch is greater than that found in any of the parthenogenetic clones. The reason why eggs develop, but fail to hatch, is unknown. In part, this may be due to the inability of the nymphs to free themselves from the oötheca. This often occurs when developed eggs lie next to, or near, undeveloped eggs. Hatching depends on the concerted effort of the mature uterine embryos which swallow air and swell; when too many remain undeveloped, some of the developed eggs cannot free themselves from the oötheca, even though the enveloping membrane is relatively thin. The BM clone in which only 47% of the embryos matured had 32% of their oöthecae with zero hatch. However, other factors probably are involved since some clones have low average hatches, yet the percentage of eggs which reach late embryonic development is high (e.g., in clone BP, an average of 27 [87%] of 31 eggs develop in an oötheca, yet only an average of 11 eggs hatch). It is possible that a lethal factor acting in late embryonic development of some clones is responsible for the low rate of hatch.

The biotic potential of the different clones of *P. surinamensis* varies, some being better reproducers than others. Biotic potential cannot be correlated with chromosome numbers alone. An advantage in one character may be offset by a disadvantage in another. For example, the clone BM has a large number of ovarioles and basal oöcytes which mature resulting in an oötheca containing an average of 45 eggs. Yet, because a low percentage of these eggs develop, and a high percentage fail to hatch, an average of only 8 individuals result from an egg case. Reproduction of different clones of *P. surinamensis* seems to parallel the results found in a study of parthenogenetic weevils; "... different populations of the same parthenogenetic weevil species having the same degree of polyploidy exhibit significant, and in some cases great morphological differences." (Suomalainen 1962).

In the Blattoidea, the phyletic line which did not evolve ovoviviparity (McKittrick 1964), only oöcyte development, oviposition by virgins, and the ability of unfertilized eggs to develop would be necessary for the evolution of parthenogenesis; retraction of the oötheca does not occur. Parthenogenesis is found in several members of the Blattoidea (Roth and Willis 1956) but these are examples of rudimentary parthenogenesis or tychoparthenogenesis (Suomalainen 1962). Obligatory parthenogenesis is not known to occur in any oviparous species of cockroach. It has been suggested that thelytoky evolved from the primitive type of tychoparthenogenesis (Suomalainen 1962). Perhaps this should be kept in mind by those involved

in pest control where sex attractants may eventually be used to decrease the male population. For example, much work has recently been reported on attempts to identify the sex attractant produced by female *Periplaneta americana* (L.). In this species, parthenogenesis may be a fairly successful temporary form of reproduction and has been carried through two filial generations without intervention of fertilization (Roth and Willis 1956).

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